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POTENTIAL APPLICATION OF BLOOD GROUPS TO PRODUCTION CHARACTERS OF CATTLE

by
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INTRODUCTION

The use of blood types in cattle for parentage analysis, twin diagnosis (both for freemartinism and for monozygotic versus dizygotic identification) embryo transference, and individual identification is well known. The major developments were made by Clyde Stormont in M. R.Irwin's laboratory (University of Wisconsin, Madison) and carried further by Dr. Stormont at the University of California, Davis and others around the world, especially in Europe.

Several attemots have been made to find associations of blood types with milk production and other characters (Rendel ,1961; Neimann-Sorensen, 1961; Connely and Stone, 1965). The B system phenogroup BO_1Y_2D' gives a bit higher butter fat in at least one breed. Several systems, A, FV, L, M, and especially the S system affect reproductive performance. For example, U' of the S system gives a higher rate of conception on first service, 64%, than its absence (dash= the absence of a detected factor) in that system which gives 50% ; see the review by Penedo, 1981.

The effect of blood type heterozygosity has not been delt with appropriately to our knowledge. Abortive attempts were started to breed cattle in order to maximize the heterosis presumed desirable for weight gain and other production characters. Typically, one attempt by Stormont with an Angus breeder ended early when the owner would not conform to the suggested breeding program. So no research has been done on the utility of blood groups to maximize the hybrid vigor implied in heterosis from Heterozygote Advantage (HA).

BASIC ASPECTS

The cattle blood typing test can be rather complex for the non-specialist. Therefore, some explanation and description is useful. The basic antibodies are produced in cattle recipients by injecting blood from donor cattle, or by injecting rabbits with blood of cattle donors. Other species are used but rarely.

Any one laboratory will not have all reagents, but will have 50-60 allowing them to identify the major groups within systems reasonably well. Often two reagents possessing the same major specificity will be used side by side. This reduces the number of check tests that may be necessary in order to interpret weak reactions or when a reagent has more than one specificity. Sometimes absorptions are not feasible to eliminate unwanted specificities, even in another system. This is because the absorption will so weaken the remaining specificity that it is not trustworthy. So a few reagents will have two factors reacting, but the duplicate reagent will have a different extra reaction seldom coincidental with the first reagents extra reaction. Rarely a trial absorption with the questionable cell type is necessary to see if it removes the critical specificity.

The B system alone will solve approximately 70% of all parentage cases commonly encountered in the USA. The 1962 report to the Purebred Dairy Cattle Association of the USA summarizing this information is suitable today.

Summary of Blood Typing Work during 7 Years (1955-1962)
by Wilmer J. Miller

Serology Laboratory, University of California at Davis
for the
Purebred Dairy Cattle Association
(Ayrshire, Brown Swiss, Guernsey, Jersey and Holstein Friesian)

Table 1. Number of samples, parentage cases and solutions.

Cases	Total
Number of samples tested	12.192
*Number of parentage cases	1.259
**Number of parentage cases solved	1.129
Percent of parentage cases solved	90 %
Number of spot checks	859
Number of exclusions in spot checks	60
Percent of exclusions in spot checks	7 %

* Omitting 28 special herd problems.
** 51 of the 130 cases not solved involved cases in which one parent was not available or bulls types elsewhere were involved. Omitting these 51 cases, the percent solved would be 1129/1208 = 93.5%

Table 2. Frequency of blood group systems critically involved in solving parentage problems

Cases	B	C	F	A	S	Z	L	J	M
1.259(*)	74%	27%	12%	12%	11%	10%	7%	6%	3%

* Approximately 90% Holstein-Friesian.

Average number of systems critically involved per case = 1.6%.

103/1259 = 8% of the cases that were not possible to solve by factor analysis were solved by phenogrouping.

With increased use of artificial insemination in cattle in the 1950's, cases multiplied in which semen from 2 or more bulls was used to "settle" (induce pregnancy in) a cow. Blood typing became the major tool for excluding or "qualifying" parents and was used frequently. Phenogroups in one system are separated by a slash, and dash ("-") indicates the absence of any detected factor (open system).

Table 3. Examples of Parentage Problems in Cattle

Example 1. Holstein-Friesian. Typical and frequent type of paternity problem.

Animal	Blood Group Systems								
	A	B	C	F	J	L	M	S	Z
Bull 1	DH	$BO_2Y_1A'E'_3G'/I_2Y_2E'_1Y'$	C_1X_1/EW	F/F	-/-	-/-	-/-	H'	Z/Z
Bull 2	D/D	$BO_1/D'E'_3F'G'O'$	$C_2EW/$	F/V	J	L	-/-	SH'/	Z/-
Dam 1	A_1/D	$BO_1/GY_2E'_1$	E	F/F	±J	L	-/-	H'	Z/-
Calf	D/D	$GY_2E'_1/D'E'_3F'G'O'$	$C_2EW/$	F/V	J	L	-/-	SH'/	-/-

Solution: The calf possesses phenogroups D, $D'E'_3F'G'O'$, C_2EW, V, SH', and dash in the Z system which must have been transmitted by the sire if the dam 1 is the true dam. Bull one lacks $D'E'_3F'G'O'$, V, SH and dash in the Z system and, therefore, is excluded as the sire. Further, neither of Bull 1's B phenogroups appear in the calf also excluding him as the sire by any dam. Bull 2 possesses the critical phenogroups and qualifies as the sire.

Example 2. Holstein-Friesian: Dam unavailable. Shows superiority of phenogrouping over factor analysis.

Bull 1	D/D	$Y_1E'_3G'Y'/Y_2A'$	X_2	F/F	J	L	-/-	H'	Z/-
Bull 2	A_1D	$O_1A'/D'E'_3F'G'O'$	$C_1E/C_1/X_1$	F/F	-/-	-/-	-/-	H	-/-
Calf	A_1D	O_1A'/FI'	$C_1E/$	F/F	J	-/-	-/-	H'	-/-

Solution: The calf possesses two B system phenogroups both missing in Bull 1 excluding him as the sire by any dam. Moreover, neither of his B groups appear in the calf also excluding him as the sire by any dam. Bull 2 possesses the B group B_1A' in common with the calf and otherwise qualifies as the sire (by a dam possessing FI', F and J).

Example 3. Holstein-Friesian. Rare case (about 6% in 1962).

Bull 1	A_1D	$BO_2Y_1A'E'_3G'/$	X_2	F/F	-/-	-/-	-/-	H'	-/-
Bull 2	$A_1(D)H$	$BO_2Y_1A'E'_3G'/B_2GO_1$	C_1E/X_2	F/F	-/-	-/-	-/-	H'	-/-
Dam 1	D/D	I_2 / E'_1	C_1X_1/X_2L'	F/F	-/-	-/-	-/-	SH'/	Z/-
Calf	D/D	$BO_2Y_1A'E'_3G'/I_2$	$C_1X_1/$	F/F	-/-	-/-	-/-	SH'/	-/-

Solution: The calf possesses D, $BO_2Y_1A'E'_3G'$, and F transmitted by the sire if Dam 1 is the true dam. Both bull 1 and bull 2 possesses the critical groups and qualify as the sire. NO solution. This is where additional systems are helpful.

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Bull 2	D/D	$BO_1/D'E'_3F'G'O'$	$C_2EW/$	F/V	J	L	-/-	SH'/	Z/-
Dam 1	A_1/D	$BO_1/GY_2E'_1$	E	F/F	±J	L	-/-	H'	Z/-
Calf	D/D	$GY_2E'_1/D'E'_3F'G'O'$	$C_2EW/$	F/V	J	L	-/-	SH'/	-/-

Solution: The calf possesses phenogroups D, $D'E'_3F'G'O'$, C_2EW, V, SH', and dash in the Z system which must have been transmitted by the sire if the dam 1 is the true dam. Bull one lacks $D'E'_3F'G'O'$, V, SH' and dash in the Z system and, therefore, is excluded as the sire. Further, neither of Bull 1's B phenogroups appear in the calf also excluding him as the sire by any dam. Bull 2 possesses the critical phenogroups and qualifies as the sire.

Example 2. Holstein-Friesian; Dam unavailable. Shows superiority of phenogrouping over factor analysis.

Bull 1	D/D	$Y_1E'_3G'Y'/Y_2A'$	X_2	F/F	J	L	-/-	H'	Z/-
Bull 2	A_1D	$O_1A'/D'E'_3F'G'O'$	$C_1E/C_1/X_1$	F/F	-/-	-/-	-/-	H	-/-
Calf	A_1D	O_1A'/FI'	$C_1E/$	F/F	J	-/-	-/-	H'	-/-

Solution: The calf possesses two B system phenogroups both missing in Bull 1 excluding him as the sire by any dam. Moreover, neither of his B groups appear in the calf also excluding him as the sire by any dam. Bull 2 possesses the B group O_1A' in common with the calf and otherwise qualifies as the sire (by a dam possessing FI', F and J).

Example 3. Holstein-Friesian. Rare case (about 6% in 1962).

Bull 1	A_1D	$BO_2Y_1A'E'_3G'/$	X_2	F/F	-/-	-/-	-/-	H'	-/-
Bull 2	$A_1(D)H$	$BO_2Y_1A'E'_3G'/B_2GO_1$	C_1E/X_2	F/F	-/-	-/-	-/-	H'	-/-
Dam 1	D/D	I_2 / E'_1	C_1X_1/X_2L'	F/F	-/-	-/-	-/-	SH'/	Z/-
Calf	D/D	$BO_2Y_1A'E'_3G'/I_2$	$C_1X_1/$	F/F	-/-	-/-	-/-	SH'/	-/-

Solution: The calf possesses D, $BO_2Y_1A'E'_3G'$, and F transmitted by the sire if Dam 1 is the true dam. Both bull 1 and bull 2 possesses the critical groups and qualify as the sire. NO solution. This is where additional systems are helpful.

Example 4. Aryshire. Note the utililty of phenogrouping.

Bull 1	$A_2D/$	-/-	X_2	F/F	-/-	-/-	-/-	H'
Bull 2	$A_1(D)$	$O_1A'/Y_1E'_3G'Y'$	C_1EX_2	F/F	-/-	-/-	-/-	H'
Bull 3	$A_1(D)H$	$BGKY_2E'_2F'O'/O_1T_1E'_3F'K'$	C_1EWX_2	F/V	±J	-/-	-/-	-/-
Dam 1	A_1D	$O_1A'/E'_3G'I'$	C_1EX_2	F/F	J	L	-/-	H'
Calf	A_1D	BO_1Y_2D'/GO'	X_2	F/V	-/-	L	-/-	H'

Solution: The calf possesses the B system phenogroups BO_1Y_2D' and GO' neither which appear in any of the putative parents including Dam 1 Nor do any of the groups of the putative parents appear in the Calf. Therefore, all are excluded as parent. (Also note the absence of S in any of the putative parents.) Fact analysis would allow bull 3 to qualify by dam 1.

Example 5. Guernsey. Are the calves Lottie and Louise Twins? Which bull is the sir

Bull 1	A_1DH	IE'_1/I'	X_2	F/F	-/-	-/-	-/-	SH'/
Bull 2	$A_1(D)$	O_1I'/O'	EW	F/F	J	-/-	-/-	SH'/
Dam 1	D/D	BI/GO_1Q	$C_1EK_2X_2$	F/F	(J)	-/-	-/-	-/-
Lottie	A_1DH	$±B±I/±G±O_1±Q/±I'/±I±E'_1$	$(±W)X_2$	F/F	-/-	-/-	-/-	±S±H'/
Louise	A_1DH	$±B±I/±G±O_1±Q/±I'/±I±E'_1$	$(±W)X_2$	F/F	-/-	-/-	-/-	±S±H'/

± signifies an atypically weak reaction

Solution: Since Lottie and Louise possess identical blood types, they are twin The atypically weak reactions in 4 of the systems indicate admixture (placenta interchange of early migratory red cell progenitors). The twins possess groups and H, I' and IE'_1, W, F, and SH' which must have been transmitted by the sire dam 1 is the true dam. (Note that the I' of the twins may have phenogroup O_1I' sin the GO_1Q phenogroup covers O_1). Bull 1 lacks W and so cannot be the sire of bo twins. Bull 2 lacks H, and IE'_1 and so cannot be the sire of both twin Together the bulls possess the critical groups, so one is the sire of one twin a the other the sire of the other twin. Which is the sire of which twin cannot decided with only this information. When the twins have offspring, their genet contribution from a particular sire should be evident.

Since these 1962 examples the number of phenogroups has double and the additional systems R' and T' added. Further, the q electrophoretic systems detecting polymorphism of hemoglobi transferrin, albumin, and carbonic anhydrase systems have been adde although they cost considerably more and are seldom needed to answ most questions. Restriction endonuclease patterns may be adapted degrees of heterozygosity leading to HA as well as solving parenta problems. But again the expense is considerable. We can confine o attentions to just the red cell systems.

In spite of all these complexities the analysis of the blood typing results is reasonably straightforward. All blood typing analyses for parentage include factor analysis. If the offspring has a particular factor, then one or both parents must possess that factor. If both putative parents lack the factor then the offspring is excluded from that parental combination. Factors are identified by a test tube reaction of red cells with a typing reagent appropriately analyzed and identified.

At least 4 of the systems, the A, B, C, and S systems have 2 or more factors inherited as a group = phenogroup. Phenogroups were first disclosed by Dr. Clyde Stormont at the University of Madison, Wisconsin. They were found to parallel the "agglutinogens" concurrently and independently disclosed by Alexander S. Wiener in human agglutination reactions of blood types. Perhaps the most impressive phenogroup is the one coded B28 which has the number one place of highest frequency in Jersey cattle (28%). B28= $BGKO_2Y_1A'B'E'_3G'K'O'Y'$

DISCUSSION

That events of heterozygote advantage might occur in nature is well known. The day moth, Panaxia, with the 3 original "species", dominula, medionigra and bimacula differing by wing spotting patterns, were disclosed to be only single gene differences (Ford,1965). But the pertinance here is that the female Panaxia preferred to mate with males of either of the 2 forms different from her. Whether one locus, or maximizing heterozygosity at several loci yields the advantage in this case is not demonstrated to my knowledge. The latter assumption seems likely.

Other examples include the white-throated sparrow, Zonotrichia albicollis, in which white-throated individuals preferentially choose tan-striped mates (Thorneycroft, 1975). A "rare male mating advantage" has been described in several Drosophila species and the house fly (Genetics 107: 577). The rare male phenotype presumably is associated with other differing loci, thus assuming an increase in heterozygosity in the progeny as well as a decrease in inbreeding.

There are species in which particular loci are adapted together to fit ecological niches. Some inbreeding is critical and necessary to maintain such groups of genes together. The Japanese quail and Vervet monkeys (Nature 295:236-237/1982 and Science 222:148/1983) are thought to fit this hypothesis. The quail, for example, prefer a first cousin over siblings, third cousins, or unrelated individuals for a mating partner.

Other species can utilize outcrossing by selective advantages of overdominance, heterozygote advantage or whatever related phrases are preferred. Perhaps cattle belong to the latter type. Have mating preferences in cattle ever been studied? Man usually imposes his will on the bulls available to the cows.

Cattle could well utilize H.A. in economic production characters. So why has no one tried? Until blood grouping only a few (often detrimental) characters were known by identified loci. Ten loci plus one more recently (T') in cattle blood groups are well known--some of them with much polymorphism. The B system is the epitome of such extreme variation in any species. As stated before over 700 phenogroups are known and this in only a relatively few breeds of cattle. For that reason alone, one could postulate that it is a complex locus, perhaps much more so than the HL-A complex in humans.

The reason for existence of such polymorphism within and among loci is only partially estimated (Miller, 1976). Contrary to our expectations from Rh information, incompatibility of blood types (mother/fetus) is an advantage in rats (Palm, 1974; Beer, 1975).

Heterozygote Advantage has been demonstrated in blood groups of chickens (Briles——). Excess of MN children from MN mothers in humans, and the FV and R'S' heterozygote excess in some cattle and bison could represent HA even though another explanation is available (Miller, 1966).

The ten or more genetic systemsof blood groups represent perhaps 1/3 of the 60 (30 pairs) chromosomes tagged. New factors could add to this. Adding several electrophoretic characters that exhibit polymorphism in cattle, such as hemoglobin, transferrrins, albumin, esterase, and carbonic anhydrase could increase this to half of the chromosomes possibly tagged with markers.

Identifying such markers in bulls could lead to better recommendations for herd sires or artificial insemination uses. Selecting for health and type by eye first, then alloting sires by maximum differences in blood types might well increase Heterozygote Advantage.

Possible Applications: Examples

Figure 1 is an example of maximizing the heterozygosity in any or all offspring of a particular cross in the Nelore breed without driving the parents to homozygosity in all systems. It is unrealistic to the extent that J homozygotes are unlikely from population frequency considerations, and the L homozygotes would be difficult to detect. Otherwise the types are reasonably typical. All progeny from this cross would be heterozygous in all 10 systems in spite of the 25 blood types possible from segregation and assortment.

The number of types possible is the product of the number of types possible in each independent system; e.g. 2 in the A system x 4 in the B system x 4 in the C system x 2 in the M system x 4 in the S system = 256.

Figure 1. Sample Nelore blood type combination to yield maximum Heterozygote Advantage (H.A.).

Male:	A_1Z'/H	$BGKY_2A'D'E'_3G'J'O'P'/BPQY_2G'P'Q'$	C_1/X_1	V/V	J/J	L/L	M1/M'	SH'/U1H'	Z/Z	R'/R'
	A_1Z'/D	$BGKY_2A'D'E'_3G'J'O'P'/PY_2A'$	C_1/R_2W	F/V	J/-	L/-	M /-	SH'/U'	Z/-	R'/S'
F1's	D/H	$BGKY_2A'D'E'_3G'J'O'P'/T_1E'_1O'$	C_1/EL'	F/V	J/-	L/-	M'/-	SH'/-	Z/-	R'/S'
	D/H	$BPQY_2G'P'Q'/PY_2A'$	X_1/R_2W	F/V	J/-	L/-	M /-	U1H'/U'	Z/-	R'/S'
	D/H	$BPQY_2G'P'Q'/T_1E'_1O'$	X_1/EL'	F/V	J/-	L/-	M /-	U1H'/-	Z/-	R'/S'
Female:	D/D	$PY_2A'/T_1E'_3O'$	R_2W/EL'	F/F	-/-	-/-	-/-	U'/-	-/-	S'/S'

The middle blood types between male and female parents represent possibilities in each system. The probablility of heterozygous offspring = 1 = 100%. There are 256 blood types possible, but all are heterozygotes in 10 systems.

In figure 2 is a sample of the possibility of knowing the maximum of Heterozygote Advantage (HA) for phenogroups in each system. Suppose the interactions of A_1DZ' and H in the A system yielded maximum HA for that system, etcetera for each system in the

hypothetical F1. (Some interactions between systems might be anticipated when we actually work on such situations. But for now we can ignore such additional complications).

So we can breed and select the homozygosity for the best phenogroups in parental stocks. While only one blood type results, all 10 loci are heterozygous.

Figure 2. Supposition of knowing the maximum H.A. for particular phenogroups and breeding P1 stocks to yield it.

Male:	A_1DZ'/A_1DZ'	$BGKY_2O'/BGKY_2O'$	C_1R_1W/C_1R_1W	F/F	J/J	L/L	M1/M1	SH'/SH'	Z/Z	R'/R'
F1	A_1DZ'/H	$BGKY_2O'/I_2PY_2E'_1G'I'Q'$	C_1R_1W/X_1	F/V	J/-	L/-	M1/-	SH'/U'	Z/-	R'/S'
Female:	H/H	$I_2PY_2E'_1G'I'Q'/I_2PY_2E'_1G'I'Q'$	X_1/X_1	V/V	-/-	-/-	-/-	U'/U'	-/-	S'/S'

Only one F1 blood type; but all 10 loci are heterozygous in the F1.

Figure 3 represents the random choice of two reasonably representative Nelore recently tested in our laboratory. If used as parents the F1 could not be heterozygous in 4 of the systems and only has a 3/128 chance of being heterozygous in as many as 6 systems.

Figure 3. Sample of the current likehood of H.A. within the Nelore breed. Two random blood types.

Male:	$A_1H/A_1(H)$	$BPQE'_3F'G'P'Q'/GA'$	$C_1R_2X_1L'$	F/F	J/	L	-/-	U1H'/	Z/-	S'
F1 #	2	4	2	1	2	(2)	1	(2)	2?	1 = 3/256
P=	.5	1	.5	0	.5	.5	0	.75	.5	0 = 0.0234+
Female:	$A_1DZ'/(A_1)H$	$BO_1I_1O'/I_2PY_2E'_1G'I'Q'$	$X_1/(X_1)$	F/F	-/-	L	-/-	SH'/U1H'	Z	S'

Number of types possible in that system from the indicated parents.
Total possible = the product of the number possible in each system.
Probability of heterozygosity in 10, 9, or 8, systems = zero; P of heterozygosity in 7 systems = ^0.0234

Blood groups, nevertheless, are better than other loci in maximizing heterozygosity in random breeding, since there are very many detected alleles in 2 of the systems and several in 2 other systems. Perhaps "Nature" intended for maximum heterozygosity often in those systems.

The reason for the existance of multiple blood group types has seldom been considered. Miller (1976) notes 4 categories of possible uses "in nature": (1) Physiological consequences including incompatibility (note that with the exception of ABO, Rh and Kell in humans incompatibility is advantageous between mother and fetus); (2) Heterozygote Advantage, per se; (3) Molecular mimicry in which parasites, especially bacteria, find it easy to mask their own antigens against antibody attack by the host in simple antigenic genetic systems but difficult when the host has controlling multiple alleles present; and (4) Cell membrane function.

Heterozygote Advantage could be involved in all of these processes.

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